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RESEARCH ARTICLE

Functional flows: an environmental flow regime benefits riparian cottonwoods along the Waterton River, Alberta

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With drainage from the Waterton-Glacier International Peace Park, the Waterton River was dammed in 1964 to trap spring flow and permit offstream diversion for irrigation. Field observations in the 1980s indicated some decrepit riparian woodlands suggesting drought stress of the black and narrowleaf cottonwoods (*Populus trichocarpa*, *P. angustifolia*) due to insufficient in-stream flows. Subsequently, an environmental flow regime commenced in 1991 and provided "functional flows," deliberately regulating in-stream flow components intended to restore ecological processes and particularly (1) an increase of the minimum flow from 0.93 to 2.27 m^3/s (mean discharge 21.9 m^3/s) and (2) flow ramping, gradual recession after the spring peak. This study investigated the historic flow patterns and the growth, population age structure, and spatial distributions of riparian cottonwoods along the free-flowing upstream and regulated downstream reaches over four dam operations intervals: the free-flowing pre-dam condition; the initial dammed interval to the mid-1970s; a post-dam and drought interval in the 1980s; and with the environmental flow regime. Analyses of sapling, shrub-, and tree-sized cottonwoods included tree ring analyses to determine ages and growth patterns, and distributions were assessed relative to streamside elevations and sediment textures. These indicated that there has been progressive cottonwood colonization after damming but the colonization band dropped in elevation with the reduced flow regime and the future woodlands could become narrower. The tree ring analyses indicated that the growth of established trees benefited from the functional flows and the increase in minimum flow was probably particularly beneficial to the riparian cottonwoods.

Key words: floodplain forest, *Populus angustifolia*, *Populus trichocarpa*, riparian restoration, river regulation

Implications for Practice

- Following evidence of riparian woodland decline along the Waterton River in Alberta, an environmental flow regime commenced in 1991, with increased minimum flows through the summer, and flow ramping, gradual recession after the spring peak.
- Analyses of tree rings demonstrated increased cottonwood growth from 1991 to 2013, probably reflecting the increased minimum flow.
- With reduced in-stream flows due to water withdrawal for irrigation, the bands of cottonwood colonization were lowered.
- This provides a promising case study for the implementation of an environmental flow regime to conserve and restore riparian woodlands.

Introduction

Cottonwoods, riparian poplars, are predominant trees in floodplain forests along rivers throughout North America and around the Northern Hemisphere (Karrenberg et al. 2002; Rood et al. 2003). The associated woodlands support rich and biodiverse ecosystems with abundant birds and other wildlife (Knopf et al. 1988; Finch & Ruggiero 1993; Hillman et al. 2016) and provide important wildlife corridors allowing movements along the river valleys and into the adjoining uplands (Naiman et al. 1993).

In semiarid ecoregions, the limiting factor for cottonwood distribution is adequate water supply and in the prairies and other dry regions, the cottonwoods are phreatophytic, obtaining their water from the alluvial aquifer (Cooper et al. 1999, 2003; Rood et al. 2011). In these regions, the floodplain water table extends almost horizontally from the adjacent river stage and rises and falls in tight association with the changing river level (Scott et al. 1999; Harner & Stanford 2003; Rood et al. 2012).

In these dry regions, dams are often implemented to provide irrigation water and the water withdrawal reduces downstream river flows and corresponding water availability for riparian woodlands (Fenner et al. 1985; Howe & Knopf 1991; Rood

Author contributions: SBR, JMM undertook the early observations; JMM oversaw the environmental flow implementation; SGF designed the study and led the field work and data analyses; SGF, SBR wrote the manuscript.

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et al. 2012). For rivers in southern Alberta, two changes in the flow regime appeared to be especially stressful for riparian cottonwoods downstream of a dam: (1) abrupt declines in river stage (level) after spring peaks and (2) extended periods of low flows through the mid- to late-summer (Rood & Heinze-Milne 1989; Rood et al. 1995). The reduced flow causes physiological stress to cottonwoods by desiccating seedlings and inducing xylem cavitation that leads to branch and crown die-back and trunk mortality (Stromberg & Patten 1996; Rood et al. 2003). With the failure in seedling recruitment and mortality of established trees, cottonwood populations have declined downstream from some dams in western North America (Fenner et al. 1985; Rood & Heinze-Milne 1989; Howe & Knopf 1991).

These effects were observed in southern Alberta along the St. Mary River where the vast majority of the riparian cottonwoods died over the past half-century, following water withdrawal that commenced around 1900 (Rood et al. 1995). The adjacent Waterton River was dammed much later, in 1964, and in the 1980s, there was evidence of woodland decline (Foster & Rood 2017). In the late 1980s, the Oldman River Dam was implemented, and as part of the environmental mitigation program for that project, there were revisions in the operations of the established St. Mary and Waterton dams, since these also influence flows along the Oldman River (Rood & Mahoney 2000; Rood et al. 2016).

The revisions to dam operations and flow coordination across the different tributaries provided the environmental flow regime that commenced in the early 1990s and was intended to sustain the freshwater ecosystems and also support human livelihoods and well-being (Brisbane Declaration 2007). As part of the environmental flow approach, specific functional flow components were implemented; these are deliberate patterns of in-stream flow regulation that are intended to sustain and restore particular ecological functions (Escobar-Arias & Pasternack 2010; Yarnell et al. 2015). For the St. Mary and Waterton Rivers, the functional flows involved two changes to address the apparent causes of the cottonwood decline (Rood et al. 2016). The legislated minimum flow downstream of the Waterton Dam was more than doubled from 0.93 to 2.27 m^3/s (*Water Act* AB Reg. 307/91) to ensure that flows would not drop below about 10% of the average natural, pre-dam discharge (21.9 m^3/s). This was intended to reduce drought stress on cottonwood seedlings and riparian woodlands, and also to improve the aquatic conditions for trout and other cold-water fish, with cooler temperatures and increased dissolved oxygen (Annear et al. 2004; Anderson et al. 2006). In addition, there was concern about abrupt flow declines that could strand fish and desiccate the rooting zones for cottonwoods and willows (Annear et al. 2004). Consequently, flow ramping was implemented to limit river stage declines to approximately 2.5 cm per day (Rood et al. 1998; Kalischuk et al. 2001).

To investigate the environmental impacts from the river damming and flow regulation, and particularly the consequences from the functional flows instituted as part of the environmental flow regime, the river flow patterns were analyzed and aerial photographs of the riparian woodlands downstream from the Waterton Dam were previously assessed and demonstrated correspondences between river flow patterns and the extent of riparian woodlands over the half-century from 1951 to 2009 (Rood et al. 1995; Foster & Rood 2017). In this complementary field study, the riparian cottonwoods along the Waterton River downstream from the Waterton Dam were investigated to assess the population age structure and growth patterns, and possible coordination with the flow patterns and local site conditions including elevation, surface sediments, and river slopes. The free-flowing upstream reach provided a reference comparison and it was expected that cottonwood recruitment along the downstream reach would correspond to the river flow patterns across the different dam management intervals and that with the environmental flow regime: (1) cottonwood recruitment would increase and (2) established cottonwood trees would display more vigorous growth.

Methods

The Waterton River

The Waterton River originates within the Waterton-Glacier International Peace Park and subsequently flows northeastward through foothills with aspen parkland to the drier prairie grassland (Fig. 1). For this study, the upstream reach commenced at the Park boundary and extended for 32 km to the Waterton Reservoir where Drywood Creek contributes about one quarter of the downstream flow. The downstream reach extended 60 km from the Waterton Dam to the confluence with the Belly River.

The sequential Waterton Lakes trap alluvial sediments from the headwaters tributaries and consequently the river bed and banks along the upstream reach are covered with cobbles with limited finer materials (Fig. 2). The major tributary is Drywood Creek, which flows into the Waterton Reservoir (Fig. 1), which would trap those sediment contributions and the banks along the downstream reach are also characterized by coarse sediments, with cobbles and gravels (Fig. 2). The upstream reach is relatively straight and flows through a narrower valley, while the downstream reach is more sinuous, with meander migration and avulsions that follow flood events and provide barren bars and islands suitable for cottonwood colonization (Foster & Rood 2017).

Historic Hydrology

River discharges (Q, mean daily values) were obtained from the Water Survey of Canada (http://www.wsc.ec.gc.ca/) for three gauges along the Waterton River and one along the Belly River (Fig. 1). From the combined records a 106 year series was developed, from 1908 to 2014. The earliest record was from the upstream reach near Waterton Park (05AD003, drainage area 612 km^2, Fig. 1A) with seasonal values (no winter measurements) from 1908, and year-round measurements after 1912. For a data gap from 1931 to 1947 values were interpolated from linear regressions with Q from the adjacent Belly River near Mountain View (05AD005, 1911–2012, D), with high correspondences for mean daily Q ($r^2 = 0.920$), maximum

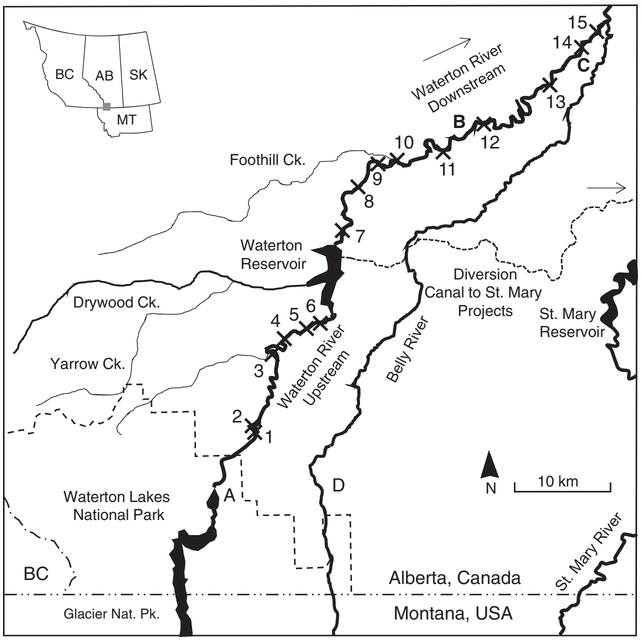

Figure 1. Map of southwestern Alberta showing the Waterton River with upstream (1–6) and downstream study sites (7–15) and gauging stations (A–C), with an inset map for location.

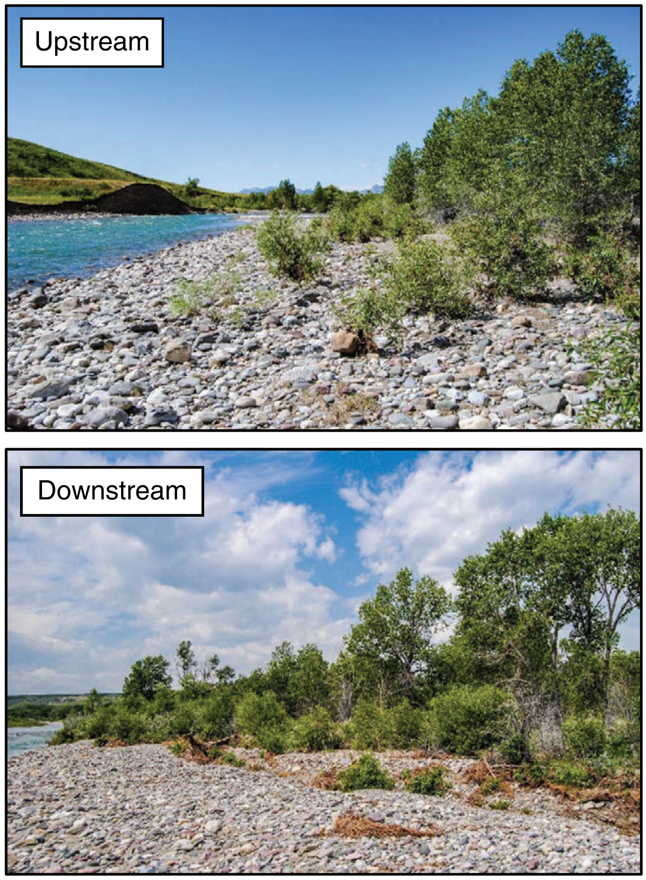

Figure 2. Photographs of typical field sites along the upstream and downstream reaches of the Waterton River in July, 2014.

mean daily (Q_{max}, $r^2 = 0.871$), monthly (Q_{month}, $r^2 = 0.965$), and growth season Q ($Q_{May\text{-}Oct}$, $r^2 = 0.921$).

Along the downstream reach, measurement near Standoff (05AD008, C) began in 1916 and continued until 1966, with a data gap between 1931 and 1934 (Fig. 1). This downstream record was extended with Q from the station near Glenwood (05AD028, from 1966, B), with close correspondences in daily Q ($r^2 = 0.978$) during the overlapping interval in 1966. These two stations have similar drainage areas (1,631 and 1,730 km^2) with no intervening tributary inflows, and the records were directly combined. To interpolate the missing 1930s data and extend back to 1908, linear regressions were undertaken between the pre-dam Standoff station and the extended upstream time series, with close correspondences: Q_{daily} ($r^2 = 0.896$), Q_{month} ($r^2 = 0.956$), and $Q_{May\text{-}Oct}$ ($r^2 = 0.861$). A lower correspondence for Q_{max} ($r^2 = 0.656$) reflected the varying inflow contributions from Drywood Creek.

Base flows were regarded as the typical annual low flow during ice-free periods prior to damming. Using a Weibull probability distribution, the peak flow with 5 year recurrence (Q_5) was considered as approximating bankfull discharge, following channel widening from ice events (Smith 1979). Peak flows exceeding the 20 year recurrence (Q_{20}) were assessed as large floods. For analyses of stage patterns, the gauging station stages were assessed and the channels at these locations appeared fairly typical, but it is recognized that the stage versus discharge relationships will vary across the transects due to the site-specific channel geometry (Shafroth et al. 1998; Willms et al. 2006). Four dam management intervals were compared: *pre-dam* (before 1963), *dammed* (or post-dam, 1964–1976), *dammed and drought* (1977–1990) and *environmental flows* (1991–2014).

Cottonwood Recruitment

To assess the suitability for cottonwood seedling recruitment, six hydrologic criteria were assessed for each reach and each year, with revisions to the method of Braatne et al. (2007) for application to the Waterton River and to recognize that the seedling establishment peak may occur separately from the flood disturbance peak (Table 1). To consider major recruitment opportunities, for the major flood years (>20 year recurrence) stage hydrographs were plotted as 3-day moving averages, and recruitment boxes with the cottonwood seed release interval and recruitment elevation that avoids scour or drought were plotted along with a 5 cm/day stage decline rate (Mahoney & Rood 1998). This would reflect the steeper stage recession at the hydrometric gauges that are positioned at bridges that confine the river and more gradual recession would probably occur at the natural, unconstrained cottonwood recruitment sites, approaching the favorable 3 cm/day (Mahoney & Rood 1998). For the upstream reach, the upper limit of the recruitment box was lowered by 50 cm to reflect the coarse substrate that would limit the capillary fringe (Mahoney & Rood 1992) and the natural flood peak attenuation downstream from the large Waterton Lakes sequence.

Field Study

In June through August 2013, field sites with gradually sloping gravel bars were accessed by hiking or rafting. Sites with limited cattle or beaver damage were preferred but these impacts were difficult to completely eliminate (Samuelson & Rood 2011). Fifteen sites were established, with six along the upstream reach and nine downstream from the Waterton Dam (Fig. 1).

At each site, two cross-sectional belt transects about 50 m apart were inventoried, each extended perpendicular from the river up to the mature woodland. These included continuous quadrats with three nested quadrat sizes: 1 × 1, 2 × 4, and 5 × 10 m to sample saplings (<0.5 m tall), shrub-sized cottonwoods (0.5–2 m), and trees (>2 m), respectively. For each quadrat, cottonwood heights and diameters were measured (calipers at ground level or 30 cm aboveground with diameter tape for trees). Quadrat distance from and elevation above the river were determined by survey with a transit and staff gauge (±1 cm) and stem densities, heights, and diameters were averaged by quadrat type, transect, site, and reach.

About 15 trees per site were randomly sampled to create diameter versus age regressions. Young trees greater than 10 cm in diameter were cut at ground level to obtain cross sectional discs. For larger trees, three increment cores were extracted at 30 cm height, the lowest position allowing auger rotation. Ring counts or annual radial increments (RI) were measured with a dissecting microscope with a Velmex stage and Acu-Rite encoder (precision 0.002 mm, Velmex, Bloomfield, NY, U.S.A.) and MeasureJ2X software (VoorTech, Holderness, NH, U.S.A.). Cottonwood rings are very faint, leading to missing rings, and false rings can reflect a growth surge within a year. Due to these challenges it is very difficult to track the specific years within a ring chronology and we generally considered 3 or 5 year averages to assess growth patterns over time. Basal area increments (BAI) were primarily analyzed to avoid the inherent variation in RI with cottonwood development (Willms et al. 2006), and were based on RI averages across the three cores. The absolute BAI varied substantially across the individual trees, partly due to the inclusion of two *Populus* species and hybrids, and proportional BAI represented the yearly BAI value/overall BAI average. This provided standardized comparisons of relative growth over the different flow management intervals.

Concentric circles were used to estimate the ages from tree cores with missed piths (Applequist 1958) and composite skeleton plots were created to identify potential false or missing rings by matching high and low growth years and correcting apparent anomalies (Stokes & Smiley 1968). Two years were added to the cored tree ages to compensate for the sampling position but there would have been variations in early height growth (Scott et al. 1999; Willms et al. 2006). Apparent ages and years of establishment for the other cottonwoods along the transects were estimated using the age and diameter regression for each reach. For comparison, the observed age structure was plotted along with cumulative yearly scores derived from the recruitment criteria analysis.

A modified Wolman pebble count was performed to determine the surface substrate texture for each site (Wolman 1954). Four hundred sediment particles were sampled along four lines parallel to the river, spaced 1 m apart. The sediments were sized by passing through a gravelometer, tallied in Wentworth scale bins, and diameter percentiles (D_x) were interpolated from the particle distribution curves. Site substrate heterogeneity was determined using the interquartile range.

Using ArcMap 10 (ESRI, Redlands, CA, U.S.A.), site distances from Waterton Park were measured using the river center line. Floodplain valley widths at each site were calculated by averaging five measurements spaced along the valley between the first contour lines present on a digital elevation map with 10 m contours.

Statistical Analyses

Linear regressions and recruitment analyses used Microsoft Excel 2013 (Microsoft, Redmond, WA, U.S.A.) and other analyses were with SPSS 21.0 (IBM Corp., Somers, NY, U.S.A.). Shapiro–Wilk tests for normality and Levene's tests for homogeneity were undertaken leading to the primary application of non-parametric tests. Mann–Whitney *U* tests were used to detect differences in tree densities and elevations between upstream and downstream reaches. Kruskal–Wallis *H* tests were undertaken to detect elevation differences between the three tree size groups followed by pair-wise Mann–Whitney *U* tests. Correlation matrices for physical and biological site characteristics were undertaken to assess correspondences across the study variables, using the Kendall τ rank-order test. A linear model analysis of variance was undertaken to assess growth, based on the proportional BAI, with two factors: interval (BAI averaged by individual tree for the interval of 1980–1990 vs. 2000–2010) and reach (upstream vs. downstream). This analysis was restricted to trees established before 1970, to avoid the slower juvenile growth following establishment (Willms et al. 2006).

Results

Hydrology

The Waterton Dam creates a proportionally small reservoir, which fills and spills in most years and consequently major flood peaks persisted downstream (Fig. 3). After each peak there was initially steep recession and the falling limb then became more gradual, often with progressive post-flood recession along the upstream reach from mid-June through July. There was a more irregular pattern in 1975, both upstream and downstream. The deliberate flow ramping commenced with the major 1995 flood but the Waterton Dam outflows need to be coordinated with regulated flows from the Oldman and St. Mary dams, creating management challenges and irregularity in the downstream stage recession in 1995 (Fig. 3). There was also unfavorable irregularity in the post-peak recession in 2005, in contrast to

Table 1. Hydrological criteria for cottonwood recruitment analyses along upstream (U) and downstream (D) reaches along the Waterton River, revised from Braatne et al. (2007).

Hydrological Component	*Criteria*	*Value*
1. Disturbance within 2 yr of a flood	$>Q_{20}$	1
Peak flow recurrence interval (Q_{year})	$Q_{10}-Q_{20}$	0.66
20 yr = 224, 447 m^3/s (U, D)	Q_5-Q_{10}	0.33
10 yr = 180, 297 m^3/s; 5 yr = 153, 243 m^3/s	$<Q_5$	0
2. Establishment peak	>2 m	1
Peak stage above base	1.3–2 m	0.66
	0.60–1.3 m	0.33
	<0.6 m	0
3. Timing of spring peak	May 24–31	0.5
Peak needs to precede or concur with seed release	June 1–15	1
	June 16–30	0.5
	Other	0
4. Stage recession rate	$M<20$	1
Moving 3-day average is stressful (5–10 cm/day), or lethal (>10 cm/day)	$M=20–30$	0.5
From peak flow or 10 June to 15 August or the day that seven consecutive mean August values occurs	$M>30$	0
Mortality coefficient (M) = (% lethal days × 3 + % stressful days)/3		
5. Drought – Late summer discharge	>August low	1
Values from typical minimum or lower quartile August discharge	August low – quartile	0.66
August low = 7.2 and 10.0 m^3/s (U, D)	Quartile – minimum	0.33
August 25th quartile = 5.1 and 6.4 m^3/s (U, D)	<minimum	0
Minimum flow criterion = 2.27 m^3/s	—	—
6. Magnitude of post-recruitment scour	<85%	1
Within 2 years following recruitment	85–115%	0.5
Scouring peak compared to Establishment peak	>115%	0

the gradual ramping in 2010 and 2014 that closely matched the intended stage recession.

Using the criteria in Table 1, the interannual recruitment scores are plotted in Figure 3 for the six criteria over the four flow management intervals. This reveals the natural variation along the upstream reach and the additional impacts of dam operations downstream. The first criterion was *disturbance* and these patterns were very similar for the upstream and downstream reaches (Fig. 4), reflecting the limited peak flow attenuation. The major disturbance event provides sediment scour and deposition to create suitable colonization sites and subsequent seedling establishment requires a sufficient *establishment peak* with appropriate *timing*. These were naturally variable and fairly similar upstream and downstream (Fig. 4).

For seedling survival, post-peak *recession* should be gradual. This was consistently favorable along the upstream reach and similarly favorable downstream before damming (Fig. 4). In contrast, after damming the stage recession was frequently unfavorable along the downstream reach. The ramping or gradual recession is especially important after high flows since this enables cottonwood and willow seedling recruitment. In 1975 there were two flow peaks both upstream and downstream, but the downstream recession exceeded the limit of 5 cm/day, as indicated with the sloped, dashed line (Fig. 3). In the subsequent flood years, recession was ideal along the upstream reach, being progressive and gradual (Fig. 3). There were unfavorable irregularities downstream in 1995 and especially in 2005, with an abrupt decline followed by a steep increase. With the implementation of environmental flows the recession ramping was more gradual, particularly in 2010 and 2014 (Figs. 3 and 4), when abundant rains reduced irrigation needs and enabled flow ramping as a management priority within the Oldman River Basin (Rood et al. 2016). In those years, flow releases from the Waterton Dam were deliberately managed to provide post-peak recessions that matched the ramping objective (Fig. 3).

Sufficient late summer flows sustain the new seedlings and thus avoid *drought*-induced mortality through that typically warm, dry and low flow interval. Late summer flows were consistently sufficient along the upstream and downstream reaches prior to damming and during the initial dammed interval when less water was withdrawn (Figs. 3 and 4). In contrast, late summer downstream flows were very unfavorable during the drought interval. With the implementation of environmental flows, the drought scores substantially improved but remained lower than along the upstream reach (Fig. 4).

Following colonization, major floods within the next 2 years would *scour* away seedlings and this criterion was quite variable and often unfavorable along both the upstream and downstream reaches, with limited alteration from river regulation (Fig. 4). The recruitment analyses indicated that two of the six hydrological characteristics, recession and drought, were especially altered with the river regulation and these were also the two flow features that were deliberately restored with the functional flow components.

Riparian Cottonwoods

Two *Populus* section *Tacamahaca* species, the black cottonwood, *Populus trichocarpa* Torr. and Gray, and the narrowleaf

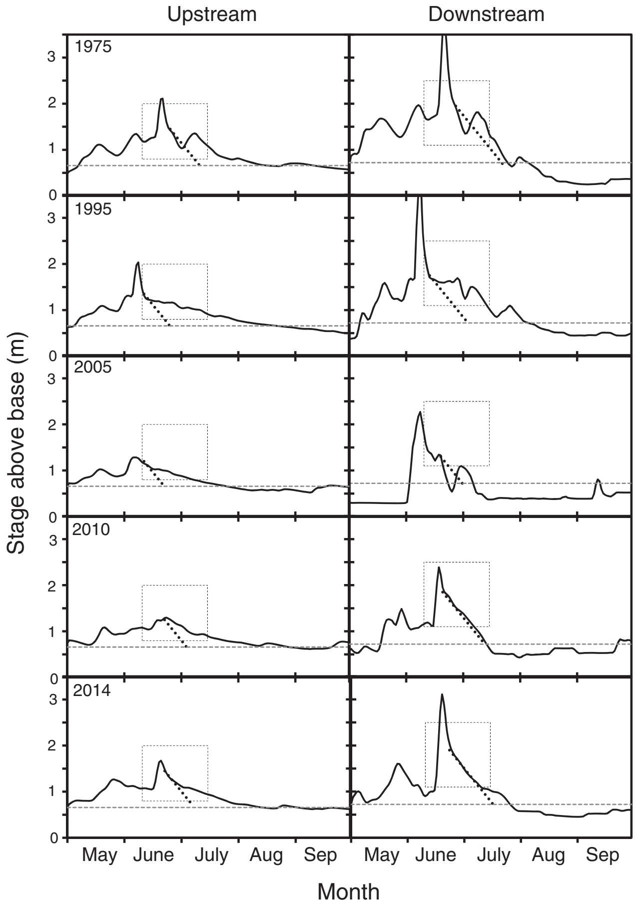

Figure 3. Stage hydrographs at the upstream and downstream gauges along the Waterton River during recent major flood years before and after the implementation of environmental flows in 1991. The dashed boxes and lines represent favorable recruitment conditions and gradual ramping, and dashed horizontal lines provide the average pre-dam August stages. This figure displays the persistence of floods following damming, and if the stage recession is steeper than the ramping objective (sloped dashed line) new cottonwood or willow seedlings would be unable to maintain root contact with the receding alluvial groundwater.

cottonwood, *Populus angustifolia* James, occur along the Waterton River system (Berg et al. 2007). No distinction was made between the species because of the extensive introgression and the challenge of discrimination during the juvenile stage when leaves are similarly narrow (Floate 2004).

The riparian woodlands along the downstream field sites generally resembled those along the upstream reach (Fig. 2). For both reaches, there were narrow bands of mature cottonwoods furthest from the river. Closer to the river, juvenile trees and smaller shrub- and sapling-sized cottonwoods were common. For further comparison, the transect cross-sections with cottonwood densities and heights are provided in Foster (2016). The upstream reach had 71 sapling, 117 shrub-sized, and 69 tree-sized quadrats with cottonwoods. Along the downstream reach, site 7 was very atypical, with extensive sand deposition over the cobble. This was the first site below the dam and near two large gravel mines, which may have impacted the sediment conditions. Consequently that site was excluded from further analyses, resulting in 81 sapling, 204 shrub-sized, and 128 tree-sized quadrats with cottonwoods along the downstream reach.

Cottonwood Age Structure and Recruitment

Increment cores from mature trees and discs from juveniles were obtained from 210 cottonwoods to determine the diameter versus age relationships, that indicated about a 0.5 cm diameter increase per year (Upstream: diameter [in cm] = (0.499 × year) + 0.927, $r^2 = 0.873$; Downstream: diameter = (0.525 × year) + 01.147, $r^2 = 0.886$; Fig. S1, Supporting Information). Some scatter probably reflects the inclusion of two cottonwood species and intermediate hybrids (Berg et al. 2007) and juveniles from seedlings versus clonal root suckers, which initially grow more rapidly (Samuelson & Rood 2004). The upstream and downstream reaches provided similar distributions and regressions with correspondences of approximately 88%, which were used to estimate the ages of the other trees along the transects.

Both reaches demonstrated progressive cottonwood establishment over the past half-century with abundant younger trees (Fig. 5), as is typical for riparian woodland recruitment (Scott et al. 1996; Dixon 2003; Samuelson & Rood 2004). Along the downstream reach, there was apparently limited recruitment in the 1960s and 1970s. There was increased recruitment in the 1980s and after the implementation of the environmental flow regime and the overall patterns were generally similar along the upstream and downstream reaches. There was limited correspondence between the apparent age structure and the recruitment scores but it is difficult to determine the specific establishment year for cottonwoods, the blending of seedling recruitment and clonal expansion complicates analyses, and the three-year groupings would further dampen the interannual patterns.

Cottonwood Growth

The increment cores from mature trees did reveal interannual coordination between river flows and cottonwood growth over the past few decades. During the initial dammed interval, the downstream BAI were lower than along the upstream reach, while the growth season flows were relatively high along both reaches (Fig. 6). With the drought interval through the 1980s, the combination of the drought and diversion along the downstream reach reduced the growth season flows, especially in the late 1980s. With the flow reduction, the growth of the downstream cottonwoods declined substantially while growth of the upstream trees was relatively unaffected. Accompanying the drought, there were many low flow days in the downstream reach, often exceeding one half of the 183 day growth season (Fig. 6).

When environmental flows were implemented the minimum flow was substantially increased and this largely eliminated the extreme low flow days, despite a regional drought in the early 2000s (Fig. 6). During the environmental flows interval there remained substantial reduction in the mean $Q_{\text{May-Oct}}$

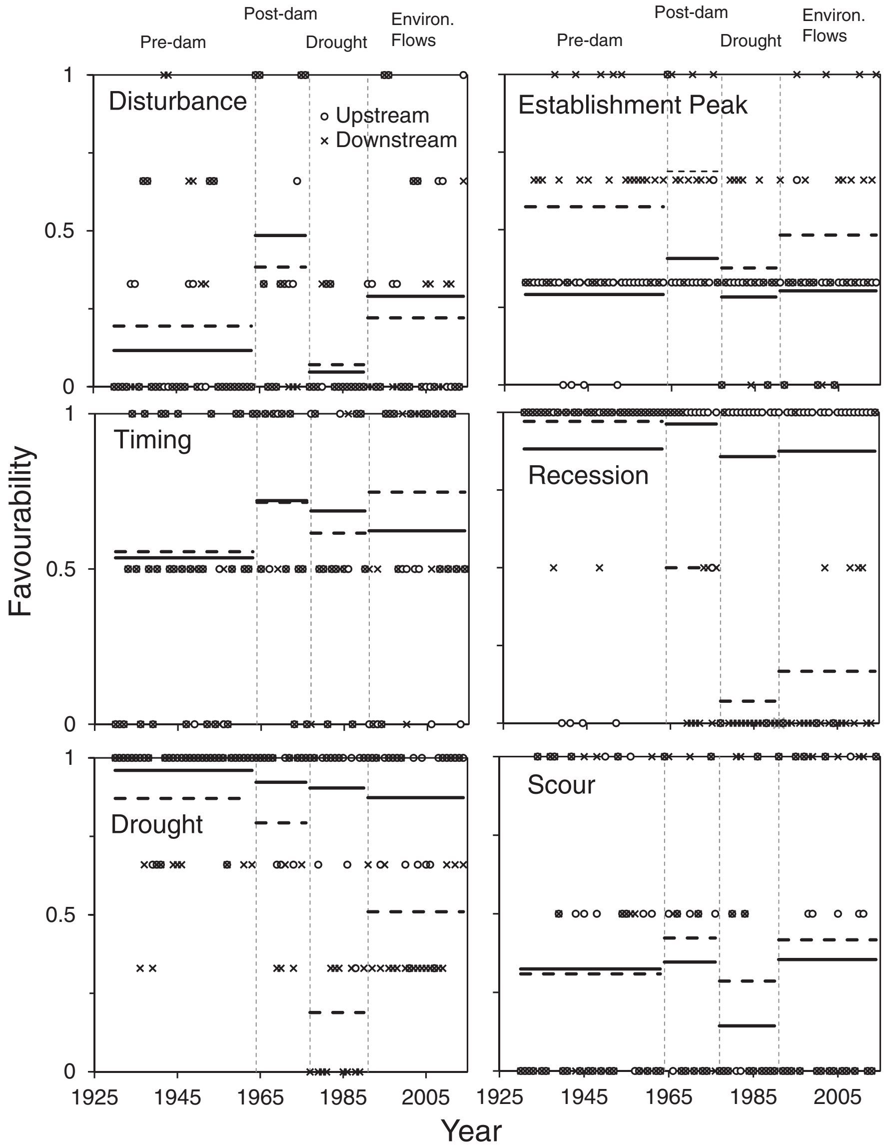

Figure 4. The interannual cottonwood recruitment scores upstream and downstream of the Waterton Dam based on hydrological criteria in Table 1. Horizontal lines indicate mean values for each management interval (solid = upstream; dashed = downstream).

for the downstream reach, due to continuing water withdrawal for irrigation. Despite this, the growth of the cottonwoods along the downstream reach increased substantially and the BAI pattern became coordinated with the growth pattern along the upstream reference reach (Fig. 6). The obvious BAI patterns (Fig. 6) were confirmed by the analysis of variance of these 10 upstream and 13 downstream trees that were established prior to 1970, thus avoiding juvenile growth (model $r^2 = 0.467$). The interval (proportional BAI were averaged by mature tree for 1980–1990 vs 2000–2010) had a significant effect ($F_{[1,42]} = 13.0; p = 0.001$) and there was a significant interval × reach interaction ($F_{[1,42]} = 18.9$, $p < 0.001$). Thus, the growth of the downstream cottonwoods was reduced during the drought interval (mean = 0.657 ± 0.072) and almost doubled with the subsequent environmental flow regime (1.267 ± 0.082), while the upstream cottonwoods displayed more consistent growth (1.019 ± 0.082 and 0.962 ± 0.082). The sequences of growth and discharge suggest that extreme low flows rather than the overall growth season flows were limiting for the growth of these riparian cottonwoods.

Cottonwood Distributions

The numbers of quadrats with cottonwood saplings, which represents the width of the bands, were similar along transects of the upstream and downstream reaches (Fig. 7, Mann–Whitney U $p = 0.972$). However, saplings occurred at lower elevations above the river along the downstream reach ($p = 0.002$). The older shrub-sized cottonwoods were more abundant along the downstream reach ($p = 0.001$) and occurred at higher elevations

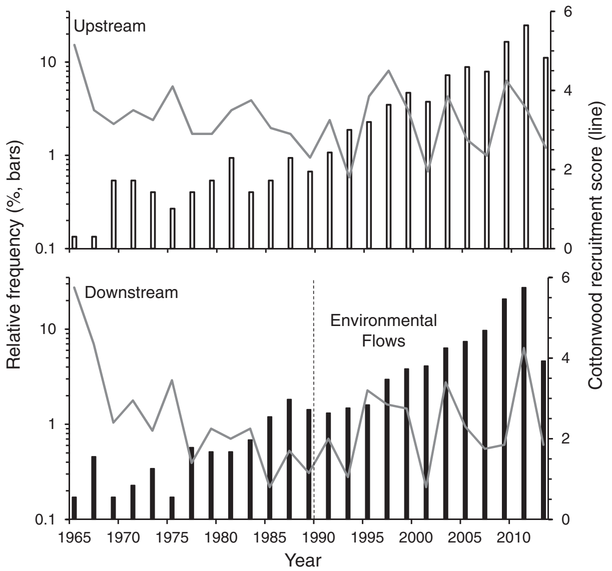

Figure 5. Apparent establishment years (moving 3 year groupings) for riparian cottonwoods along upstream and downstream reaches of the Waterton River. The cottonwood recruitment scores are also plotted (Table 1), with higher values indicating more favorable flow patterns.

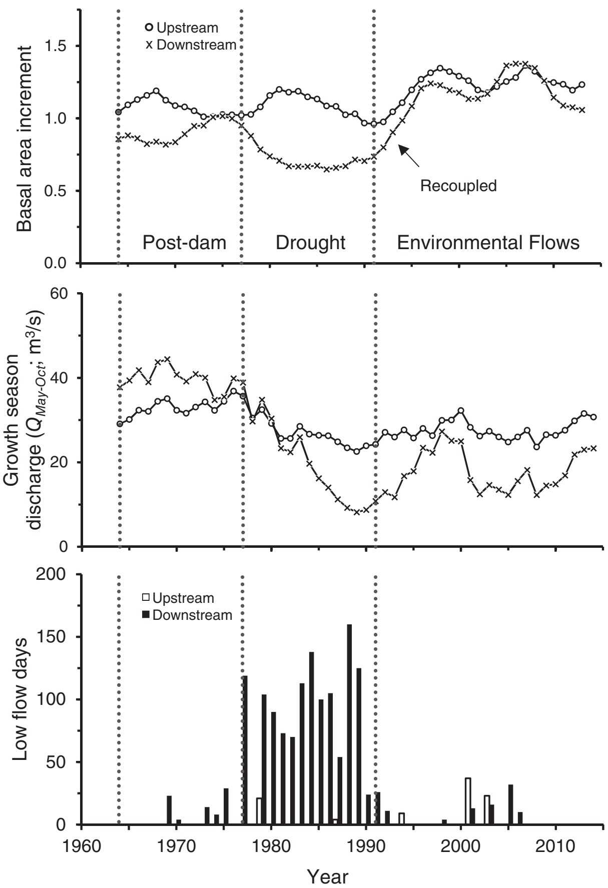

Figure 6. The 5 year averaged proportional basal area growth increments from cottonwood trees along the Waterton River during three water management intervals (top; SE = 0.196 (upstream) and 0.137). Mean growth season discharge (5 year moving averages, middle) and number of low flow days recorded (<2.27 m^3/s; bottom) upstream and downstream of the Waterton Dam.

than along the upstream reach ($p = 0.005$) and in higher positions than the downstream saplings (Fig. 7). There was a trend toward broader tree distributions along the downstream reach ($p = 0.094$) and these occurred at higher elevations than the shrub-sized cottonwoods along the downstream reach (Fig. 7). This demonstrates a difference in the elevational distributions between the two reaches. Narrower bands that contained mixed saplings, shrub- and tree-sized cottonwoods occurred along the upstream reach. In contrast, there was more banding along the downstream reach, with the older and larger cottonwoods occurring at higher positions and further from the river (Fig. 7 and Foster 2016; cottonwood size groupings: $\chi^2 = 32.26$, $df = 2$, $p = <0.001$; Mann–Whitney: sapling and shrub $U = 5{,}115$, $p < 0.001$; sapling and tree $U = 3{,}009$, $p < 0.001$; shrub and tree $U = 11{,}781$, $p = 0.134$). Thus, following damming and diversion, the downstream cottonwoods were colonizing lower positions.

Physical Site Characteristics

The cottonwood recruitment distributions and elevations appeared to be influenced by the sites' physical attributes (Table 2), but these factors apparently had limited influence on the diameters or heights of the cottonwoods (Foster 2016, Appendix C). The physical characteristics that corresponded with recruitment are presented for the downstream reach that was impacted by damming and river regulation (Table 2).

The sediment textures were correlated with physical attributes, becoming finer along the longitudinal river corridor and with broader floodplain zones, but coarser with steeper river slopes (Table 2). Cottonwood recruitment was correlated with sediment texture, increasing with finer sediments (Table 2, negative correlations). Sites that contained larger sediments also generally had increased texture heterogeneity, and decreased cottonwood densities (Table 2). Sites that contained finer sediments supported higher densities of cottonwoods and generally allowed cottonwood establishment at higher elevations (Table 2). Linking hydrogeomorphic characteristics, locations along steeper river slopes were associated with coarser sediments and reduced occurrences and elevational positions of cottonwoods.

Discussion

The hydrogeomorphic requirements for cottonwood colonization are reasonably well understood (Scott et al. 1996; Auble & Scott 1998; Karrenberg et al. 2002; Polzin & Rood 2006) and case studies with restorative responses support the ecological understanding (Shafroth et al. 1998; Hall et al. 2011; Tiedemann & Rood 2015). These requirements include aspects of hydrology and physical site characteristics, with differentiation and refinement across the different cottonwood species and hybrids (Rood et al. 2003; Wilding et al. 2014). In southern

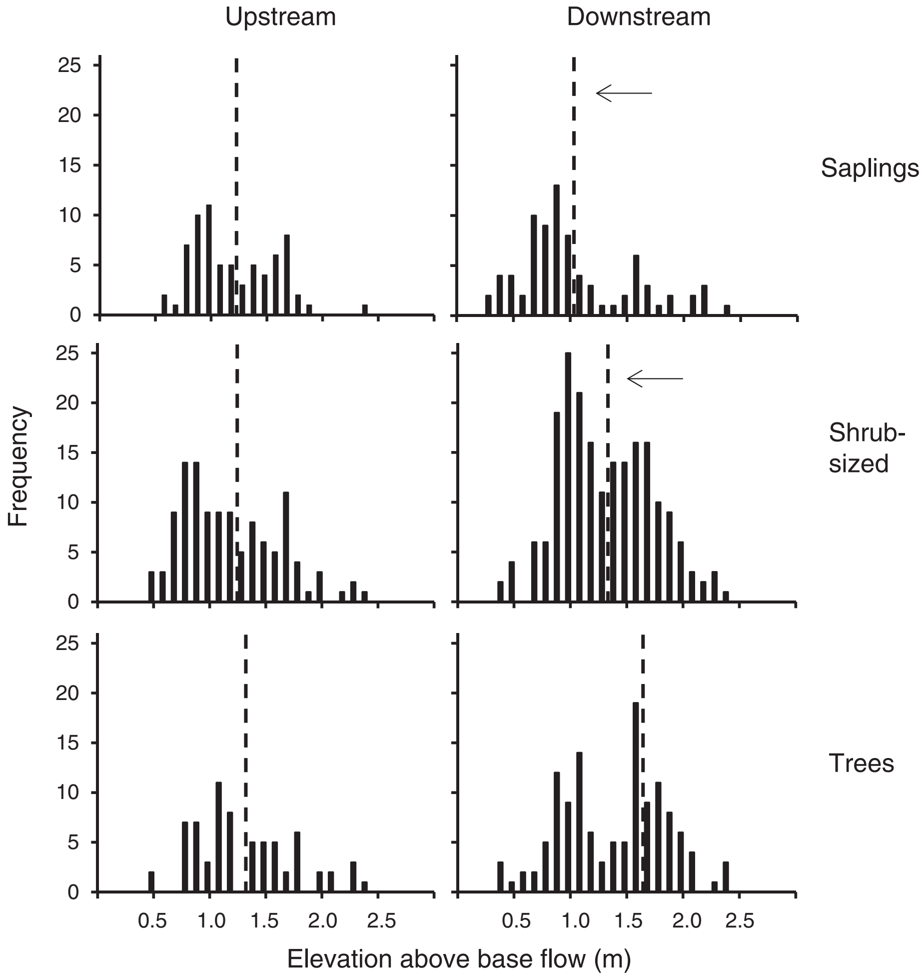

Figure 7. Elevational distributions of quadrats containing cottonwood saplings (top), shrub-sized juveniles (0.5–2 m tall; middle) and trees (bottom) along the upstream and downstream reaches of the Waterton River. The dashed vertical lines provide median values and arrows indicate apparent downward shifts in elevation downstream from the Waterton Dam.

Alberta, the collapse of cottonwoods along the St. Mary River prompted the implementation of the environmental flow regime in association with the implementation of the Oldman River Dam, and for all three major dams in the basin (Rood & Mahoney 2000; Kalischuk et al. 2001).

The environmental flow regime particularly included changes in the two functional flow components, the minimum flow that was provided especially through the warm and dry interval of mid- to late summer and flow ramping, gradual post-peak recession. The prior development and implementation of the functional flow strategy followed from our provisional interpretation that these two components were likely to be particularly important and the systematic analysis in this study supports that interpretation. For this analysis, we modified the method of Braatne et al. (2007) to refine a quantitative approach that would be applicable for other regulated rivers with riparian cottonwoods or other groundwater and disturbance dependent trees and shrubs (Richter & Richter 2000; Dixon 2003; Andersen 2005). We revised the flow thresholds slightly and added an additional criterion for the establishment peak, to recognize that seedling colonization often occurs over a few years following a major flood disturbance event (Scott et al. 1996; Polzin & Rood 2006).

Of the hydrological requirements, floods provide the essential geomorphic disturbance to produce extensive barren nursery sites through scour, transportation, and deposition of the alluvial sediments (Scott et al. 1997; Richter & Richter 2000; Polzin & Rood 2006). Of the major post-dam floods along the Waterton River, only the flood of 1964, during the initial reservoir filling, was substantially attenuated (Rood et al. 1995). Otherwise, major floods have persisted along the downstream reach. This would not be the case along rivers with proportionally larger reservoirs that substantially attenuate floods (Tiedemann & Rood 2015). For many other regulated rivers, flood attenuation is a top priority in dam operation and it is unlikely that this essential fluvial component would be restored.

Along the Waterton River, the downstream forest age structure did not display an age gap, indicating that cottonwood recruitment persisted after damming. This probably reflects a combination of seedling recruitment and clonal suckering,

Table 2. Kendall's τ correlations between seven physical conditions ($n = 8$ sites) and six cottonwood characteristics ($n = 16$, two transects per site) across the study sites along the downstream reach of the Waterton River ($t = p < 0.1$; $* = p < 0.05$; $** = p < 0.01$; negative correlations are in blue, positive in red).

	Distance	Floodplain Width (FPW)	River Slope (RS)	Sediment D_{16}	Sediment D_{50}	Sediment D_{84}	Sediment Heterogeneity	Density (D) Sapling	Density (D) Shrub-Sized	Density (D) Tree	Elevation (E) Sapling	Elevation (E) Shrub-Sized	Elevation (E) Tree
Distance		**0.429***	−0.071	0.000	−.357^{t}	**−0.786****	**−0.571****	**0.541****	0.251	0.175	0.178	0.168	0.267
FPW			−0.357^{t}	**−0.429***	**−0.50***	−0.357^{t}	−0.286	0.342^{t}	0.147	0.123	0.089	0.186	0.018
RS				**0.50***	**0.571****	0.143	0.071	−0.108	−0.234	−0.368^{t}	**−0.658****	**−0.577****	**−0.462***
D_{16}					0.357^{t}	0.071	−0.143	0.108	0.095	−0.088	−0.302	−0.279	−0.142
D_{50}						**0.429***	**0.50***	−0.324^{t}	−0.320^{t}	−0.193	−0.373^{t}	−0.372^{t}	−0.373^{t}
D_{84}							**0.786****	**−0.541****	−0.320^{t}	−0.158	−0.196	−0.242	**−0.409***
Heterogeneity								**−0.541****	−0.320^{t}	−0.018	−0.071	−0.112	−0.267
Sapling D									0.288	0.089	0.090	0.122	0.027
Shrub-sized D										0.366^{t}	0.207	0.316	0.345^{t}
Tree D											0.341^{t}	**0.393***	0.358^{t}
Sapling E												**0.649****	**0.584****
Shrub-sized E													**0.677****

which is prolific for black and narrowleaf cottonwoods. Floods scour the stream banks and floodplains, causing root scarification that induces adventitious suckering, which contributes to the population but does not include sexual reproduction and genetic recombination, which is essential for long-term adaptation. While the functional flow component of gradual flow ramping might have promoted seedling recruitment, the overall population patterns along the upstream and downstream reaches were generally similar.

The other functional flow component was the increase in the minimum flow. Although overall growth season flows remained relatively low in the drought intervals, when inflows were low and irrigation demands were high, the functional flow regime eliminated the extreme low flow days. Probably due to the associated reduction in drought stress, the annual growth of the cottonwood trees was increased and matched that along the free-flowing upstream reach. This suggests that the growth and health of riparian woodlands is especially impacted by severe low flow events and that sufficient minimum in-stream flows would be beneficial for conservation and restoration.

While it was uncertain whether the environmental flow regime promoted cottonwood recruitment, the younger cottonwood seedlings and saplings along the downstream reach were established at lower elevations than prior to damming or along the upstream reach. This probably reflects the general reduction of in-stream flows due to the water withdrawal for irrigation. This may provide an initial, downward expansion of the cottonwood bands, but in the longer term the future woodlands might be in narrower bands that are positioned closer to the river channel. This response would match the predicted pattern that would follow from reduced in-stream flows either due to river damming and water diversion, or following seasonal declines due to climate change (Rood et al. 2008; Stromberg et al. 2010). Downward vegetation expansion and river channel narrowing have been observed following damming along other rivers of western North America, although the specific responses are also influenced by other factors (Johnson 1994; Friedman et al. 1998; Wilding et al. 2014). Woodland narrowing is less certain and changes in the width of cottonwood bands have varied across other rivers and reaches (Rood et al. 1995; Johnson et al. 2012; Scott et al. 2013).

The particular local geomorphologic characteristics will influence the channel and cottonwood responses, partly due to influences on water availability (Scott et al. 1999; Willms et al. 2006). In this study, river slope and valley width influenced sediment texture and subsequently cottonwood abundance. Cottonwoods grow on a wide range of sediment textures but finer substrates increase water retention and seedling colonization (Mahoney & Rood 1992; Kalischuk et al. 2001; Cooper et al. 2003).

Implications for River Resource Management

This study indicated that the environmental flow regime with the specific functional flow components benefited the riparian cottonwoods downstream from the Waterton Dam. Cottonwood recruitment might have been promoted with the deliberate flow ramping, gradual post-peak recession, although this possible benefit was uncertain. Flow ramping can have relatively little impact on the annual water balance and is probably most important in high flow years, when wet conditions benefit cottonwood seedling recruitment and reduce irrigation demands, increasing the flow management opportunities (Richter & Richter 2000; Rood et al. 2016).

The functional flow strategy promoted the growth of young and older cottonwoods, probably particularly due to the increased minimum flow. This does require some additional water commitment for the environmental allocation and will thus have some cost relative to water resource management. Sufficient minimum flows are probably especially important in the warm and dry summer interval of low flow years, when insufficient in-stream flows would impose drought stress on the riparian woodlands (Stromberg & Patten 1991; Rood et al. 1995; Scott et al. 1999). These insufficient flows would lead to water warming and depleted dissolved oxygen levels, stressing trout and other cold-water fish and thus the environmental allocation will similarly benefit the aquatic and riparian ecosystems (Anderson et al. 2006). The increased minimum in-stream flows also provide other important benefits including the improvement of water quality through the dilution of contaminants and for the Waterton River, the increased minimum flow allowed additional hydroelectric power generation and facilitated irrigation water pumping from the lower Waterton River, and especially from the Belly River downstream. With this range of environmental, social, and economic benefits, the increased minimum flow becomes readily justifiable.

The Waterton River system thus provides a promising and instructive case study for the implementation of environmental flows as a strategy to conserve and even restore river and riparian ecosystems. From this success, we strongly encourage the consideration of similar implementation of functional flow components such as flow ramping and sufficient minimum flows for other regulated rivers, especially in dry regions where the floodplains support the only native woodlands.

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. Trunk diameters versus tree ages for cottonwoods along the upstream and downstream reaches of the Waterton River.

Figure S2. Sediment distributions and heterogeneity ($D_{75} - D_{25}$) at sites downstream from the Waterton River (locations shown in manuscript Figure 1) and the associated floodplain widths.

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